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EFFECT OF LIGHT UPON THE GERMINATION OF SPORES AND THE GAMETOPHYTE OF FERNS.

BY A. C. LIFE.

While germinating fern spores in 1905 at the Missouri Botanical Garden, for the purpose of producing material for a morphological study, it was noticed that different intensities of light had a decided effect upon germination. A perusal of the literature revealed conflicting results by different investigators. It was then thought worth while to verify the work, or at least attempt to clear up the discrepancies of the earlier investigators. Consequently, in the early part of 1906, experimentation was begun with different intensities of light.

HISTORICAL.

The earliest definite experimentation upon the effect of light upon fern spore germination was that of Borodin in 1868. He worked mainly with the spores of *Aspidium spinulosum* and *Aneimia phyllitidis*, and was not able to obtain germination in darkness. The exposure of some of the spores to light after they had been in the dark 18 days, was sufficient to bring about germination in 9 days after they were removed from darkness. He also experimented with spores of *Asplenium, Allosorus, Polypodium* and *Phegopteris,* and obtained no germination in the dark. Schmidt also was not able to secure germination of the spores of *Aspidium violascens* and *Aspidium filix mas* in the absence of light. His work was in 1870, two years later than that of Borodin.

Goeppert in 1869 germinated spores of *Osmunda* in darkness, while Kny in 1872 could not verify his results.

Schelting in 1875 reported germination of *Pteris aquilina, Aneimia phyllitidis,* and two species of *Aspidium* in darkness at a temperature higher than the ordinary room temperature. In 1878, in his experiments with *Scolopendrium*, Beck found that light of a certain intensity was necessary for the germination of the spores. The spores of *Equisetum,* with respect to the effect of light upon their germination, were experimented with by Sadebeck. He reported that light is not necessary for their germination.

The germination of the spores of liverworts was worked upon in 1876 by Leitgeb. He found that they neither germinated in darkness nor very weak light. When germinated in light they formed a germ-tube which was slightly negatively geotropic.

More recently Forest Heald in 1898 carried out a valuable line of experimentation upon moss, fern, liverwort, and equisetum spores. He secured germination of moss spores in darkness by using either a sugar or a peptone solution as a culture medium. Fern spores, especially those of *Ceratopteris thalictroides* and *Alsophila Loddigesii*, were made to germinate at a temperature of 32° C. He was not able to cause liverwort spores to germinate in darkness in sugar solution at higher temperatures. He attributes his failure to the effect of bacteria which grew in his cultures. Equisetum spores germinated readily in ordinary media at ordinary temperature in the dark.

In 1901 Schulz obtained results that in some respects were contradictory to those of Heald. He does not regard the swelling of the moss spore in the sugar solution without light as normal germination. Spores were germinated in blue as well as yellow light, but required 30 days instead of 20 days, the time required in yellow light. No germination of fern spores in darkness at 30°-35°C was obtained, contradictory to the work of Heald. To determine this, he worked with spores of *Gymnogramme chrysophylla*, *Aneimia phyllitidis*, and *Alsophila australis*. However, he was able to germinate *Ceratopteris thalictroides* in 3 days in darkness at 30°-35°. This agreed with the work of Heald.

Treboux in 1905 verified the work of Heald in the germination of moss spores in sugar solution. He was also able to secure germination in inorganic solutions. Further, he found that the gemmae of *Marchantia* would grow into prothallia in both organic and inorganic solutions in the absence of light.

In 1907 Laage reported that a great many species of ferns were able to germinate in darkness in both sugar solutions and inorganic solutions, especially Knop's solution. However, *Alsophila australis*, *Asplenium lucidum*, and *Polypodium aureum* could not be induced to germinate in darkness under any conditions. Laage further claimed that there was no new formation of chlorophyll in darkness.

The Ophioglossaceae are reported to germinate in darkness. Hofmeister found prothallia of *Botrychium lunaria* three inches beneath the surface. Arcangeli reports the germination of *Pilularia*, and Woronew the same for *Marsilia* in the absence of light. Each of these investigators of the water ferns claims there is new formation of chlorophyll in the absence of light, especially in the germination of the megaspore.

Much less work has been done upon the effect of light upon the prothallium and sex organs than has been done upon germination. In 1879 Prantl reported that strong light produced a growth of archegonia, of course on the shaded side of the prothallium, and that weak light tended to produce only antheridia. The effect of light upon the dorsiventrality of prothallia had been worked upon earlier by Prantl and others.

METHODS.

The spores which were sown in the progress of this experimental work were almost all collected at the Missouri Botanical Garden, and sowed soon after collection. They were collected at any and all times of the year, and germinated almost as well in winter as at other seasons. The *Alsophila australis* spores germinated after a rest of about a year after collection. The spores of other ferns which were worked with, germinated well when sown as soon as they were thoroughly dry.

The spores were nearly all germinated in specially prepared boxes with sliding glass covers. These boxes were filled to a depth of about six inches with sterilized garden soil. The pots in which the spores were sown were imbedded in this soil, to a depth of about two-thirds of their height. To determine the best medium upon which to sow the spores, experiments were made with sand, garden soil and leaf mold. From these experiments it was found that leaf mold was the best medium, of those experimented with, for the germination of the spores. In preparing the pots for sowing the spores, they were filled to a depth of about an inch and a half with either coarse cinders or broken pieces of pots. Upon this a layer of garden soil was placed which extended to within about an inch of the top of the pot. This soil layer was then covered with a layer of sifted leaf mold to within about a quarter of an inch of the top. The pots were then thoroughly sterilized in a Koch steam sterilizer. Just before sowing the spores the pots were completely saturated with sterilized water. After the spores had been sown, glass plates were placed over the pots and they were imbedded in the germination boxes. The pots were not watered directly, but the soil surrounding them was kept well moistened.

Two special germinating boxes were prepared; one for germination in strong light, and the other for germination in absence of light. The box for strong light had a glass front and cover, and was painted white on the inside. The box for germination in darkness was constructed so as to exclude light and at the same time to allow some access of air. This was accomplished by means of a closely fitting sliding cover which overhung the lower part of the box one end of which was perforated. A thermometer was placed in the cover of this box. Petri dishes were also used for germinating spores. Two or three thicknesses of filter paper were placed in each of them, and they were then filled about one-third full of 0.5% Knop's solution, and sterilized before the spores were sowed. These cultures, as well as some upon leaf mold, were kept in an incubator at a temperature of from 30° to 33° C. As a means of exposing the spores to one-sided illumination during germination, black paper was placed upon Petri dishes, leaving an opening on one side for the entrance of light.

The intensity of the light was determined by a light meter used for determining the time of exposure in photographic work. The time required for bright sunlight to change the sensitive paper to the standard tone was taken as the unit.

By the method used by Wiesner, other intensities of light were determined by a comparison of the time required to produce the normal tone with the time taken in bright sunlight. A number of observations were taken of each intensity of light and the intensities given in this paper are the averages of these observations. The intensities are those of sunlight or diffuse daylight, as artificial light was not used; in fact, natural conditions of light were more nearly simulated than can be done by artificial light.

INFLUENCE OF LIGHT OF DIFFERENT INTENSITIES UPON GERMINATION.

Before giving the results of the experiments upon different intensities, the effect of entire absence of light will be given. Spores of *Dicksonia apiifolia* upon leaf-mold were sowed February 3, 1906, and on February 3, 1907 were examined and found not to have begun germination. This culture was then exposed to light and division took place within about 8 days, and in about 20 days the surface was green with the young prothallia. Thus spores were able to germinate after having been in a moist dark chamber for an entire year. Another sowing of *D. apiifolia* started February 19, was transferred to light September 29, and germinated by October 10. A culture of *Alsophila pruinata* was sowed and transferred to light at the same time as the *Dicksonia,* and germinated by October 8. Sowings of *Aneimia phyllitidis* and *Gymnogramme calomelanos Mertensii* were kept in darkness 40 days without germination, while the control from the same groups of spores germinated in 10 days.

Sowings of *Asophila pruinata* and *Aneimia phyllitidis* were made upon leaf-mold and exposed to a temperature of 30°-33° C. in darkness during a period of 41 days for the *Alsophila* and 40 days for the *Aneimia.* Neither germinated in the absence of light even at the higher temperature. The *Alsophila* culture was transferred to light, and germinated in 11 days, while the control of the *Aneimia* germinated in about 10 days in light.

In 0.5% Knop's solution in darkness at 30°-33° C., a sowing of *Gymnogramme calomelanos Mertensii* germinated in 20 days. A sowing of the same species in leaf-mold at room temperature did not germinate in darkness in 40 days.

In very diffuse light of 0.002 intensity, the spore coats of *Alsophila pruinata* burst, but germination went no further during a period of six months. No change took place in *D. apiifolia* in the same time, and no germination began in either *Aneimia phyllitidis* or *Asplenium filix foemina* in three months.

To determine the effect of different light intensities upon length of time required for germination, *Alsophila pruinata*, *A. australis* and *Dicksonia apiifolia* spores were used in the experiments.

Cultures in leaf-mold, of *A. pruinata*, were placed in different intensities of light, and the time required for germination was noted. Temperature and moisture were made as nearly equal as possible in all the cultures. They were all in the same green-house, exposed to a temperature varying from 18° to 24° C. In light intensity of 0.15, first division, which is a definite point in germination and is used to designate germination in this paper, took place in 25 days.

In light intensity of 0.075, division or germination began in 12 days. In light of 0.02 intensity there was no germination in 25 days, in fact the spore coats were just bursting.

Two series of *Dicksonia apiifolia* were grown. The first was sowed on September 29, and examined on October 15, On this date the spore coats of those in light 0.15, had just begun to burst, while those in the weaker light of 0.075 intensity had begun to germinate.

The second series was sowed on November 24, and on December 15, after 11 days, the spores of the culture in light 0.075 had divided, and some of them were well along in germination. At the same time the spore coats of those in light 0.15 had just begun to burst. The spore coats of those in weaker light of intensity 0.02 did not burst until the fifteenth day, while those in light 0.075 germinated in 8 days.

A series of spores of *Alsophila australis* was sowed on September 27, and examined on October 24. The spores from light intensity 0.15 had germinated and formed young prothallia of from 2 to 3 cells. Those in light 0.09 had grown into prothallia of from 5 to 12 cells, and those in light of the intensity 0.02 had divided and formed prothallia of from 2 to 5 cells. The difference in the effect of light of the intensity 0.15 and 0.09 was very marked on November 14, when the culture grown in the latter intensity was bright green, while the surface of the culture grown in the more intense light showed very little color.

From these experiments it is readily seen that these fern spores germinate most readily in a light intensity of from 0.075 to 0.09, and that both great and low intensities of light are not as favorable for germination as medium intensity. Of the fern spores used in this experimental work, none were able to germinate upon leaf-mold in absence of light, neither were they able to germinate in very weak light.

Alsophila pruinata and *Aneimia phyllitidis* could not be induced to germinate in leaf-mold in darkness at a temperature of 30°-33° C. This is contrary to the results of Heald, who germinated a species of *Alsophila* and other ferns, among them *Ceratopteris thalictroides*, at a temperature higher than the ordinary laboratory temperature.

Schulz was able to germinate *Ceratopteris thalictroides* in darkness at a higher temperature; but was not able to secure germination of the same species of *Alsophila* that Heald worked upon. Neither was he able to germinate any other species in darkness at a higher temperature. He thinks *Ceratopteris* is capable of germinating in darkness because it has a water habit, such as the Marsiliaceae, which germinate in darkness according to Arcangeli and Woronew.

Laage, in some recent work upon germination, claims higher temperatures have a retarding effect.

The germination of *Gymnogramme* in 0.5% Knop's solution is not exceptional, as Laage secured germination of a number of ferns in both organic and inorganic solutions in absence of light. In his valuable work he shows what strengths of various solutions are most favorable for germination in darkness. However he was not able to germinate *Alsophila australis*, *Asplenium lucidum*, and *Polypodium aureum* under any conditions in absence of light.

According to the results of several investigators, the stimulus to germination and to growth which in nature is given by light may be given by either organic or inorganic solutions.

Examination of the chlorophyll content of the spores used in the experiments, was made with the result that all of them contained more or less chlorophyll. *Alsophila pruinata* spores have more chlorophyll than *Alsophila australis* and germinate much more readily.

Laage in his work with chemical solutions found that *Osmunda* spores germinate more readily than other spores, which no doubt is partially due to their having a larger chlorophyll content.

Some work has been done by Heim and Schulz upon the effect of different parts of the spectrum upon germination, but very little upon the effect of different intensities of white light.

EFFECT OF LIGHT OF DIFFERENT INTENSITIES UPON THE PROTHALLIA AND REPRODUCTIVE ORGANS.

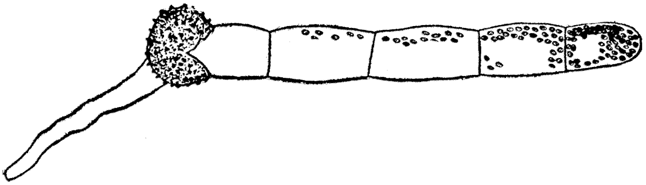
First the effects of absence of light will be given. Prothallia of *Dicksonia apiifolia* that were grown in light favorable for the production of archegonia and which bore them abundantly, were placed in darkness and left there three months. Although they were covered with water, as were also the cultures in light, to insure the freeing of the sperms and the possibility of their reaching the archegonia, no sporophytes developed. Control cultures in light under other similar conditions bore sporophytes in abundance. At the end of the three months the prothallia were paler than when placed in darkness, but still contained abundant chlorophyll. Antheridia developed upon the upper surface near the margins of the prothallia. This production of antheridia in darkness is exceptional and, as far as my experiments were conducted, took place only in mature prothallia that were placed in darkness.

Spores of *Aneimia phyllitidis* and *Asplenium filix foemina* were first germinated in light and when the prothallia, in the two- or four-celled stage, were transferred to darkness, it was found that they had increased some in length, and that the cells were more elongated than when placed in darkness. The extremities of these tubular or filamentous prothallia contained considerable chlorophyll, but the basal cells contained none, or only a trace. The starch had also disappeared from all the cells.

After germinating in light of considerable intensity, cultures of several kinds of ferns were transferred to light of an intensity of about 0.002, very diffuse light, when in the 2-4 celled stages.

Dicksonia apiifolia produced elongate prothallia some of which were from 2-4 cells in width near the tip. *Alsophila pruinata* grew out into tube-like forms. *Aneimia phyllitidis* grew into tube-like and more branching prothallia. The disappearance of the chlorophyll from the base and the grouping of it near the tips was very noticeable in the *Aneimia* cultures.

Cultures of *Asplenium filix foemina* did not elongate so much as the others, and all the cells contained abundant chlorophyll. None of these cultures produced antheridia in this intensity of light, although they remained from two to three months under this condition.



1. GERM-TUBE OF ANEIMIA SHOWING CHLOROPHYLL CONTENT OF CELLS, × 100.

Cultures of the same species as mentioned above were germinated in light and then transferred to stronger light than that of the former experiments, of an intensity of 0.008. In this condition the cultures produced antheridia but no archegonia.

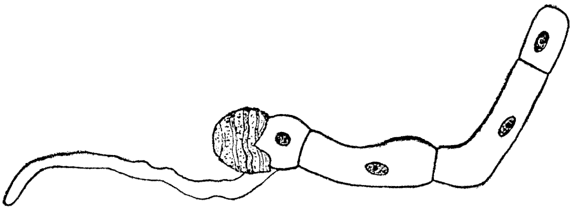
A specially abundant crop of antheridia was produced in a culture of *Alsophila pruinata.* This culture was first grown in weak light and while still yet having no antheridia was transferred to a position where the light was from above and of an intensity of .01. Within about a month antheridia developed abundantly over almost the entire under surface of the prothallia.

Prothallia of *A. pruinata* germinated and grown in light of an intensity of 0.3 had abundant archegonia but no antheridia. About 25 of these prothallia were sectioned and no antheridia were found upon any of them. Later on this culture was transferred to weaker light and antheridia developed. Some of these prothallia took such a position with reference to the light that they were about equally illuminated on both sides, with the result that archegonia were produced on both sides.

A noticeable effect of different intensities of light upon the form of the prothallium was observed especially in *Alsophila pruinata.* In very diffuse light of 0.002 intensity the growth was a somewhat branched filamentous form. In stronger light of 0.008 intensity, the prothallia grew out into ribbon-like forms and bore only antheridia. In these no trace of a meristematic cushion upon which archegonia develop, was to be found. In still stronger light the expanded heart-shaped prothallium was produced which bore both archegonia and antheridia. In more intense light of 0.3 intensity, archegonia but no antheridia were produced upon heart-shaped prothallia shorter than those in weaker light.

Cultures of *D. apiifolia, Asplenium filix foemina,* and *Aneimia phyllitidis* produced both archegonia and antheridia when grown in light varying from 0.03 to 0.3 intensity.

Cultures of *Aneimina phyllitidis* and *Gymnogramme calomelanos Mertensii* were exposed to light from one side only in Petri dishes containing 0.5% Knop's solution. Both of the cultures produced tubular prothallia that were positively



2. GROWTH OF GYMNOGRAMME GERM-TUBE WITH LIGHT FROM ONE SIDE, AND THEN SHIFTED ABOUT 90°, × 100.

heliotropic By shifting the culture of *Gymnogramme* about 90°, a bending of the prothallia was observed in a direction toward the light, while the rhizoids turned from the light.

Some work upon the effect of different intensities of light upon the prothallia and reproductive organs was done by Prantl in 1879. He reported that in weak light only antheridia were developed upon the prothallia. His work was with *Aneimia phyllitidis, Polypodium vulgare, Osmunda regalis,* and *Aspidium filix mas.* However, he did not give the intensities of the light to which he subjected the prothallia.

Klebs' work in 1893 is verified in the main by my results. By weak light he obtained branching prothallia with adventitious growths and with *Pteris aquilina* he secured a thread-like growth, resembling that of *Trichomanes* normally. In strong light heart-shaped prothallia were produced which bore both archegonia and antheridia.

Furthur work along the line of my investigation is that of Heim. He experimented with strong and weak white light, as well as yellow, blue and violet rays of the spectrum. In strong light he grew heart-shaped prothallia that produced both archegonia and antheridia. He reports the best growth of prothallia in daylight reduced 20-25%. In weakened light, but he does not say how much, elongate prothallia were produced which bore both archegonia and antheridia. The cultures in yellow light grown by him produced long and narrow prothallia with antheridia but no archegonia.

The blue and violet rays of the spectrum were the same as the reduced light, slackening the growth and producing adventitious prothallia. His results are of interest because the yellow light had the same effect as white light of tolerably small intensity in producing only antheridia. Here I wish to say that my cultures producing antheridia remained so for about six months, with no sign of archegonia upon them.

The effect of nourishment upon the archegonia and antheridia was worked upon by Prantl in 1881 with the result that the archegonia could be suppressed by nourishment lacking in nitrogen.

This is interesting in that it shows that other factors than light may enter into the problem. It is very probable that anything that lowers the vitality or interferes with the usual life processes may inhibit the production of the archegonia.

In some unpublished work by Shattuck at the University of Chicago, upon the Marsiliaceae, it has been found that light may inhibit the production of the megaspores.

Spores were exposed to light from one side only to see if they exhibited the polarity reported by Stahl for *Equisetum* spores, but they gave only negative results. These same cultures did show the marked heliotropism before mentioned. This heliotropism was observed some years ago by Sachs, Prantl, and others, and Wiesner (81) has worked out a theory for such heliotropism based mainly upon turgor. Leitgeb (76) reports positive heliotropism for liverwort prothallia.

To show that fern spores are capable of germinating independent of photo-synthesis, Schulz germinated spores in air free of carbon dioxide, in the presence of light. He claims in this germination the oil of the spore is converted into starch by the stimulus of light. We may infer, from the fact that a number of investigators have gotten starch formation in darkness by cultivating spores in both organic and inorganic solutions, that these solutions give a stimulus to the transformation of the substances in the spore to starch. Laage takes the position that there is no new formation of chlorophyll in germination in darkness. This is contrary to the results of Schelting upon germination of the spores of ferns, and to Bittner as well as Schimper upon the ferns in general. From the fact that *Equisetum* spores, which contain an abundance of chlorophyll, are able to germinate readily in darkness at ordinary temperatures as shown by Heald, and spores that have most chlorophyll form a young prothallium with more chlorophyll than those with less chlorophyll, the view of Laage is a very plausible one. It is noticeable that the chlorophyll in the spore has a different form of plastid from that of the young prothallium, the plastids of the spore being much smaller and sometimes apparently little more than granules.

SUMMARY.

1. Under ordinary conditions spores of Cyatheaceae and other ferns experimented with, do not germinate in darkness when sowed upon leaf-mold.
2. Higher temperature than ordinary room temperature was not sufficient to induce germination of *Alsophila pruinata* and *Aneimia phyllitidis* in darkness.
3. Germination was best in light of medium intensity, about 0.075 sunlight.
4. Intensity of light affects form of prothallia, weaker light producing filamentous or ribbon-like prothallia, while strong light produces heart-shaped prothallia in all except *Aneimia*, which has a lateral growing point.
5. Strong light of intensity of 0.3 causes production of archegonia only in *Alsophila pruinata*, while in other ferns worked with, archegonia and antheridia were produced.
6. Weak light inhibits the production of archegonia and favors the production of antheridia.
7. Young stages of the prothallia of *A. pruinata*, *Aneimia phyllitidis*, and *Gymnogramme* are strongly and positively heliotropic.

In conclusion I wish to express my thanks to Professor Wm. Trelease and Professor S. M. Coulter for valuable suggestions in the preparation of this paper.

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